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LATE BLIGHT RESISTANCE WORK IN SCOTLAND[1]

W. Black[2]

Late blight in Scotland leapt into prominance fully a century ago when in 1845 and '46 it attained epidemic proportions and destroyed much of the potato crop. The potato by that time had become a staple food plant. These years of potato famine came to be known as the "Hungry Forties," a description which applied to Western Europe in general and to Ireland in particular where privations and hardship were extremely severe. Since then the disease has been a permanent if intermittent menace to the crop and only occasionally during that period could the damage caused by it be described as negligible.

Although the search for blight resistant varieties had been in progress all that time, it was not until 1909, when Dr. Salaman at Cambridge demonstrated the heritable nature of resistance in a wild species, *S. edinense*, that the possibility of overcoming the disease was placed on a scientific basis. Dr. Salaman later employed *S. demissum* as the source of resistance and made considerable progress in the breeding work that followed Salaman (8).

In Scotland *S. demissum* was first introduced into breeding experiments by the late Dr. Wilson at St. Andrews in 1908, but no records of tests for resistance to blight appear to have been made. It is possible that Dr. Wilson did not appreciate the resistance qualities of the species and that he had other reasons for its use in hybridizations. At any rate some of his material which was presented to the Scottish Plant Breeding Station in 1921 was later found to be unaffected by the disease and to possess reasonably good commercial qualities in other respects. This material was widely employed in breeding experiments for a number of years until eventually it was realized that the resistance it possessed was inadequate to give permanent protection.

The first indications of the extraordinary resources of the parasite came to light in 1932 when blight appeared in both England and Germany on seedling selections that had hitherto been regarded as immune from the disease, Salaman (9), and Muller (6). This apparent breakdown in resistance was found to be due, not to any change in the plants, but to the arrival of a new specialized race of the parasite. The situation had thus completely altered, and it was necessary to breed for resistance to this new race as well as to the original one.

For this purpose the work at the Scottish Plant Breeding Station started afresh by crossing *S. demissum* with commercial varieties and employing the backcross method to improve yielding capacity and other essential qualities. Although apparently possessing the desired resistance

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to blight, this material proved unsatisfactory for genetical work on account of the irregularity of the chromosome numbers, Black (1). In an attempt to overcome this difficulty *S. demissum*, which is hexaploid in constitution, was crossed with the diploid species *S. rybinii* in 1937. A single seed was obtained, giving a fertile tetraploid hybrid which in turn was crossed with commercial varieties to produce a series of fertile hybrids. Repeated back-crossing to commercial varieties then followed. In this material chromosome behavior was normal, segregation ratios were more typical of Mendelian inheritance, and early maturity was a feature of some of the blight resistant segregates.

As these experiments progressed and as more races of the parasite were isolated, it became possible to distinguish the different types of resisters produced. Repeated back-crossing to commercial varieties had the effect of separating the different genes controlling the resistance inherited from the wild species. It became clear that the freedom from blight enjoyed by *S. demissum* was not due to immunity in the strict sense but more accurately to the hypersensitivity of its cells. The parasite was able to penetrate the tissue of all plants alike, but in some it was localized at the points of infection by the rapid formation of a necrotic barrier, and no further damage occurred. These hypersensitive plants may be described as "field immune" to conform with the terminology adopted for a similar response to virus X found in certain varieties such as Epicure and King Edward, and to distinguish such a reaction from "field resistance" which some varieties of *S. tuberosum* possess. Field resistant varieties, such as Champion, Ackersegen, Stormont Dawn and Furore are attacked by late blight but the damage caused is relatively less severe than in most other varieties of *S. tuberosum* grown under similar conditions. This partial protection appears to be determined by a complex of morphological and physiological characters which limit the rate of infection and the subsequent development and sporulation of the fungus. It may be observed under field conditions by the longer time required by the parasite to reach a specified degree of infection. Genetically speaking, field resistance is presumed to be controlled by a series of minor genes which determine the degree of susceptibility in susceptible varieties and the extent of necrosis in field immune forms. In contrast with field immunity, field resistance gives partial protection against all the specialized races of the parasite that have arisen in the search for hypersensitive varieties.

Since field immunity, as found in *S. demissum*, appeared to offer the possibility of complete control of the disease, the breeding experiments were designed to follow up that aspect of the problem. In the course of the investigations four major genes controlling hypersensitivity to blight were distinguished, and these were named R_1, R_2, R_3, and R_4, Black (2). Gene R_1 was first found in the breeding material gifted by Dr. Wilson. The plants so constituted remained free from blight for a number of years but eventually they were attacked by a new race, designated B. A search for field immunity from both the common race and the new one was readily found in seedling derivatives of *S. demissum* x *S. tuberosum*, and the gene controlling it was named R_2. A few years later these AB resisters, as they were described, succumbed to a further specialized race which was labelled C. This race attracted special interest when it was found to be ineffective against Dr. Wilson's B-susceptible material.

Thus it transpired that R_1 genotypes were hypersensitive to races A and C and susceptible to B whereas R_2 genotypes were hypersensitive to A and B and susceptible to C. Obviously the difference between these two genotypes was of a qualitative nature.

The next steps in the investigations as indicated by these findings were, firstly, to combine genes R_1 and R_2 in order to attain field immunity from all three races A, B and C, and secondly, to search for new and more powerful genes. The former was accomplished without difficulty by intercrossing R_1 and R_2 plants and selecting the survivors of tests involving the three races. The selections so produced have not yet been attacked by blight under field conditions in Scotland. Meanwhile a new gene, designated R_3, was found in progenies bred from the triple-hybrid material *(S. rybinii* x *S. demissum)* x*S. tuberosum*, which remained unscathed by all three races, A, B and C. These R_3 genotypes have also remained free from blight in Scotland.

In the course of the experiments with the triple-hybrid material certain selections became blighted in the field. Tests revealed that both the plants and the race attacking them were different from those already known. The gene concerned was accordingly named R_4 and the parasite race D. Tests involving the R_4 genotype also revealed that two different races had unwittingly been labelled B; one of them was ineffective against the R_4 genotype, whereas the other caused disease. These two forms were therefore designated B^1 and B^2, respectively.

In Scotland, therefore, 4 independent genes controlling hypersensitivity to blight have been distinguished. The races found locally in Scotland number 5, *viz.*, the common race A and 4 specialized races, B^1, B^2, C and D.

During recent years isolates of *Phytophthora infestans* occurring in various territories overseas, particularly in Africa, were forwarded for identification. Among them were found 6 new races, *viz.* E and F from Tanganyika sent by Dr. G. B. Wallace, G and H from Kenya sent by Dr. R. M. Nattrass and I and J from Peru sent by Mrs. Bazan de Segura. It should be emphasized that these races are not necessarily confined to the countries mentioned for since that time some of them have been found elsewhere. Further, all the races isolated from field plots in Scotland have also been represented in the cultures from overseas. Two races distinct from any of the above were received through the kindness of Dr. Mastenbroek in Holland. Altogether the list of distinct races employed for experimental purposes in Scotland now numbers 13.

With the help of these imported races it was possible to analyze a large number of progenies bred from known genotypes involving all four R genes and many different gene combinations. Each gene was found to be inherited independently in simple Mendelian fashion and, by means of appropriate hybridizations, the combination of all four genes in a single plant seemed a straight-forward breeding operation. In order to study this more closely one of the progenies bred from R_1R_2 x R_3R_4 genotypes, was raised, and each clone was tested for its reaction to all the available races of the parasite. Sixty-four seedlings were thus examined for their reaction to *11* different races, and the genes inherited by each were ascertained as far as possible. Theoretically 16 different genotypes are expected in such a cross, and they should be distributed in equal

proportions. The figures obtained (Table 1) indicate that this did in fact occur. They were readily classifiable into 13 different categories, but owing to the lack of certain additional races it was not possible to distinguish R_1R_3 types from $R_1R_3R_4$, R_2R_3 from $R_2R_3R_4$, and $R_1R_2R_3$ from $R_1R_2R_3R_4$. Since these double groups contained twice as many plants as the single groups, there is little doubt that the complete range of genotypes was represented in the progeny. This conclusion is further supported by the segregation ratios obtained with each of the races involved (Table 2): The common race gave a 15 : 1 segregation, races B^1,H,J and D a 7 : 1, races G, B^2 and C a 3 : 1, and races N8, F and N9 gave a 1 : 1 segregation of resistants to susceptibles in accordance with expectation.

TABLE 1.—*Distribution of genotypes in progeny bred from R_1R_2 X R_3R_4; 64 plants tested with 11 different races.*

Genotype	Number of Plants	
	Observed	Expected
r	5	4
R_1	7	4
R_2	4	4
R_3	4	4
R_4	5	4
R_1R_2	2	4
R_1R_3	10*	8*
R_1R_4	3	4
R_2R_3	8**	8**
R_2R_4	2	4
R_3R_4	4	4
$R_1R_2R_3$	8***	8***
$R_1R_2R_4$	2	4
$R_1R_3R_4$	10*	8*
$R_2R_3R_4$	8**	8**
$R_1R_2R_3R_4$	8***	8***

*Double group consisting of R_1R_3 + $R_1R_3R_4$ genotypes.
**Double group consisting of R_2R_3 + $R_2R_3R_4$ genotypes.
***Double group consisting of $R_1R_2R_3$ + $R_1R_2R_3R_4$ genotypes.

Although the genetical aspect of the problem has been interpreted on a disomic basis, it is not presumed that chromosome associations are invariably of this type. The species *S. demissum* as shown by Lehmann (5) and others gave evidence of disomic inheritance in intraspecific hybridizations, and this hypothesis proved convenient in analyzing the

TABLE 2.—*Segregation ratios obtained in progeny bred from R_1R_2 X R_3R_4.*

Progeny 2070		Parentage R_1R_2 x R_3R_4	
Race	Observed R : r	Expected R : r	Theoretical R : r
A	59 : 5	60 : 4	15 : 1
B¹	52 : 12	56 : 8	7 : 1
H	55 : 9		
J	55 : 9		
D	54 : 10		
G	46 : 18	48 : 16	3 : 1
B²	44 : 20		
C	48 : 16		
N8	34 : 30	32 : 32	1 : 1
F	26 : 38		
N9	32 : 32		

earlier generations following interspecific crossing. In later generations a few atypical segregations have occurred according to Black (2). These consisted of progenies derived from resistant parents that were duplex for a particular gene and the segregations obtained were intermediate between normal disomic and tetrasomic expectation. The figures suggested that both allosyndesis and autosyndesis may occur in this essentially allotetraploid material and that segregations depend upon the relative frequency of each. A mixed inheritance of this nature is not unexpected in interspecific hybrids involving three distinct species that are not wholly compatible and have differences in chromosome number. The choice of a theoretical basis for studying inheritance lies between a disomic and a tetrasomic structure, each with deviations from the normal. The former has been retained throughout the investigations as the more convenient and possibly the more accurate basis for studying this polyploid material.

The nature of the inheritance of the four R genes, individually and in combination, have been studied in relation to the various physiologic races of the parasite that have been isolated and identified by Black (2). As a result of this genetical information, together with the observed reactions of the parent plants to the different races, it has been possible to compile a table to illustrate the interrelationships between genes and races (Table 3). This table contains all the combinations involving the presence or absence of the four genes. Each gene when present is limited in the table to the simplex condition since dominance prevents the differentiation of higher values, at least by the simple test techniques employed. This series of genotypes provides a genetical basis for the classification of races of the fungus, and the relationships so illustrated

TABLE 3.—*Interrelationships of genes and strains*

Genotypes	Strains of *Phytophthora infestans*															
	A	B¹	H	J	D	G	E	B²	—	C	I	—	N8	F	N9	
	0	1	2	3	4	12	13	14	23*	24	34	123*	124	134	234	1234*
r	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
R1	—	+	—	—	—	+	+	+	—	—	—	+	+	+	—	+
R2	—	—	+	—	—	+	—	—	+	+	—	+	+	—	+	+
R3	—	—	—	+	—	—	+	—	+	—	+	+	—	+	+	+
R4	—	—	—	—	+	—	—	+	—	+	+	—	+	+	+	+
R1R2	—	—	—	—	—	+	—	—	—	—	—	+	+	—	—	+
R1R3	—	—	—	—	—	—	+	—	—	—	—	+	—	+	—	+
R1R4	—	—	—	—	—	—	—	+	—	—	—	—	+	+	—	+
R2R3	—	—	—	—	—	—	—	—	+	—	—	+	—	—	+	+
R2R4	—	—	—	—	—	—	—	—	—	+	—	—	+	—	+	+
R3R4	—	—	—	—	—	—	—	—	—	—	+	—	—	+	+	+
R1R2R3	—	—	—	—	—	—	—	—	—	—	—	+	—	—	—	+
R1R2R4	—	—	—	—	—	—	—	—	—	—	—	—	+	—	—	+
R1R3R4	—	—	—	—	—	—	—	—	—	—	—	—	—	+	—	+
R2R3R4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	+
R1R2R3R4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+

*Hypothetical races — Resistant
+ Susceptible

provide a means of calculating the segregation ratios to be expected from the mating of any pair of genotypes in the series when infected with any race or group of races of the parasite.

It will be seen from the table that each gene controls hypersensitivity not only to the common race but also to a particular group of specialized races. The known specialized races, on the evidence of these relationships, are classifiable in three distinct orders according to the number of different major genes that are impotent against them. The first order (races B¹, H, J and D) is pathogenic on the presence of 1 major gene; the second order (races G, E, B², C and I) is pathogenic in the presence of two major genes; and the third order (races N8, F and N9) is pathogenic in the presence of three major genes. A fourth order is also envisaged, capable of attacking plants with four major genes, but so far no such race has been found.

This classification provides a means of correlating each race with the particular host genotype that appears to be the natural host of the race in question, *i.e.* the host upon which the race should attain maximum growth and reproductive capacity. The natural host of each race may be found by means of the diagonal of susceptibility signs in the table, *e.g.* the natural host of race H is genotype R_2; of race C, genotype R_2R_4; and of race F, genotype $R_1R_3R_4$. It should be noted however, that such races are also capable of attacking certain other plants, less well endowed with resistant genes.

Black (3) has shown that some evidence exists that specialization usually progresses by steps from one order to the next, toward a wider host range. Thus the common race may give rise to first order specialized races, which in turn may give rise to second order races and so on. There is also circumstantial evidence that second, and even third order races may have arisen directly from the common race, omitting the intermediate phases. Whatever may be the normal method, it is clear that changes occur not only towards a wider host range but also in the reverse direction.

One of the most pertinent questions relating to the late blight problem is the mode of origin of new races. There appears to be two schools of thought; one favors physiological adaptation, the other, mutation. It is generally agreed that the fungus is relatively unstable, but it is becoming more widely recognized that changes cannot be affected at will. The fact that new races have been obtained in planned experiments does not exclude mutation or the selection of mutant types. But repeated failure to effect change (Black, 3; Muller, 7; Bonde, *et al.* 4) strongly suggests that mutation plays a significant role. Limited modification without nuclear change can, no doubt, take place, resulting in quantitative differences in vitality and aggressiveness. But such modification can hardly account for the qualitative differences between races that are now so well known. If differences were quantitative only, then specialized races having a wider host range would be more virulent and would cause greater damage to varieties of *S. tuberosum* than the common race. The reverse has been found to be true. When mixtures of races were grown on *S. tuberosum* in competition with each other, those with the widest host range tended to disappear after a limited number of passages. Such races are obviously not fully adapted to the environment of *S. tuberosum* and their reproductive capacity is lower. If this were not so, the common race would tend to disappear and be replaced by the particular race that could grow and reproduce most rapidly on commercial crops of *S. tuberosum*.

The selective ability of the various genotypes towards the different races appears to be an important factor in considering methods and techniques for the maintenance and multiplication of cultures. If the natural host is used for each race, the cultures may be maintained more readily at normal equilibrium with less risk of change in their pathogenicity.

So far 14 of the 16 genotypes listed in the table have proved susceptible to one or more of the races collected. Of these genotypes, 13 represent the natural hosts of the 13 races, whereas the 14th genotype, *viz.* R_2R_3, is susceptible to a third-order race. Accordingly, only two genotypes, $R_1R_2R_3$ and $R_1R_2R_3R_4$, have not been attacked in the experiments.

In view of these circumstances, it seems clear that the search for new and more powerful genes must continue. It is likely that further new genes will be found and further new races of the parasite will appear. Whether permanent freedom from blight will ever be attained is unknown. If the fungus is potentially capable of causing disease on all so-called resistant species, then the sooner we can prove it, the better. That is the justification for testing resistant seedlings in territories where conditions favor evolution of the parasite, and for importing and classifying every new form that arises. Meanwhile we must continue on the assumption that economically valuable resistance can be bred into varieties suitable for commercial purposes and that food production must benefit accordingly. We know very little about the persistence of these specialized races under natural conditions, or the effect of different climatic conditions upon them. These and other aspects of the problem merit consideration and may have a bearing on the commercial future of so-called field immune varieties.

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INTERVEINAL MOSAIC OF POTATO[1]

D. S. MacLachlan,[2] R. H. Larson[3] and J. C. Walker[3]

Tubers of the potato varieties Irish Cobbler, Green Mountain, and seedling 41956 infected with interveinal mosaic were obtained from E. S. Schultz, United States Department of Agriculture, Beltsville, Maryland. The symptoms produced by the interveinal mosaic virus on seedling 41956, at 18° C., although resembling those caused by virus A infection, were generally more severe; but on Green Mountain they were of a mild type. A mild interveinal chlorosis was evident in Irish Cobbler.

The term interveinal mosaic was first used by Quanjer (6) in Holland in 1923 to describe a virus disease of the British variety Duke of York. Systemic symptoms consisted of a distinct interveinal chlorosis, and a slight upward rolling of the leaf edges. These symptoms closely resembled those of potato leafrolling mosaic as described in the same year in Maine by Schultz and Folsom (8). In 1932 Murphy and McKay (5) compared American and European interveinal mosaic by graft inoculation to Green Mountain and found the two to be identical. They stated that "no particular attention appears to have been paid to this disease in America, although it occurs there." It was demonstrated (1) that Quanjer's original interveinal mosaic was incited by a combination of two viruses, virus X and the aphid transmitted tuber blotch virus (virus F) which incited a tuber necrosis in President.

McKay and Dykstra (4), in Oregon, in 1932 first used the term interveinal mosaic in the United States to describe a virus disease of the American varieties Irish Cobbler, American Wonder and Triumph. They stated that the symptoms on these varieties corresponded to those originallly described by Quanjer (6), and were also identical with those of the super mild mosaic reported by Young and Morris (9) in Montana in 1930. In 1951, Schultz (7) indicated that the symptoms of interveinal mosaic in Green Mountain and Irish Cobbler were readily masked by high temperature. He reported infection of 15 to 30 per cent with the virus in fields of Green Mountain and Irish Cobbler and indicated that yield reductions of 13 to 18 per cent resulted.

In the present study an attempt was made to transmit interveinal mosaic mechanically and by aphids (*Myzus persicae* (Sulz.))* to a number of plant species susceptible to virus A (2, 3). In no case were systemic

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*Non-viruliferous aphids (*Myzus persicae*) used in these experiments were maintained on tobacco plants (*Nicotiana tabacum* var. Havana 38) in insect-proof cages.

symptoms or local lesions observed on the following species: *Physalis floridana* Rydb., *P. peruviana* L., *P. angulata* L., *P. viscosa* L., *P. virginiana* Mill., *Nicotiana rustica* L., *N. glutinosa* L., *N. tabacum* L. var Havana 38, *Solanum nigrum* L., *S. dulcamara* L., *S. pseudocapsicum* L., Cockerham's *S. demissum*, Köhler's *S. demissum*, *Lycopersicum esculentum* (L.) Mill. var. Stokesdale, *L. pimpinellifolium* (Jusl.) Mill., *Capsicum frutescens* L., *Callistephus chinensis* (L.) Nees, and *Vigna sinensis* (Tornes) Savi.

Although no symptoms were observed on *Nicandra physaloides* (L.) Gaertn., this species proved to be a masked carrier of the interveinal mosaic virus, being infected both mechanically and by aphids.

The potato varieties Irish Cobbler, Green Mountain, British Queen and seedling 41956** were readily infected when mechanically inoculated with expressed sap from infected plants of seedling 41956. At 24° C. symptoms were masked, but at 18° C. inoculated plants were stunted and exhibited a marked interveinal chlorosis with a slight rugosity of the leaves as shown in figure 1. Similar symptoms developed following aphid inoculation.

When Irish Cobbler and British Queen were grafted with scions of seedling 41956 recently infected with interveinal mosaic and held at 18° C., no top necrosis resulted in either variety. Systemic symptoms, however, were similar to those resulting from mechanical and aphid inoculations. Grafts with scions from the same source were also made on young plants of *Datura stramonium* var. *tatula* (L.) Torr. and *D. ferox*. After 3 weeks, *D. stramonium* var. *tatula* exhibited numerous small, well-defined, chlorotic spots on the lower leaves. About 3 weeks later, the symptoms changed and on chlorotic leaves appeared as large, dark green, circular lesions each surrounding a chlorotic center as you will note in figure 2. More diffuse, chlorotic spots were observed on *D. ferox* 4 weeks after grafting and remained unchanged.

Plants of *N. physaloides* in the third-leaf stage were inoculated by means of viruliferous aphids, and held for 20 days at 24° C. When scions from these inoculated plants were grafted on young plants of *D. stramonium* var. *tatula* and *D. ferox*, symptoms typical of interveinal mosaic resulted.

The relation between the interveinal mosaic virus and virus A was determined by cross protection experiments using *N. physaloides* as a test species. Ten plants in the third-leaf stage were aphid-inoculated with interveinal mosaic virus and 10 uninoculated plants served as controls. Twenty days after the initial inoculations, 5 of the plants carrying interveinal mosaic virus were mechanically inoculated with a virulent strain of virus A (2, 3). At the same time 5 of the control plants were also inoculated, and the remaining 5 plants served as healthy controls. Ten days after the second inoculation, symptoms typical of the virulent strain of virus A appeared on the inoculated controls. Similar symptoms were also observed on plants inoculated first with interveinal mosaic virus and subsequently with virus A. No symptoms appeared on plants inoculated with interveinal mosaic virus alone in accord with the results reported above which showed that *N. physaloides* is a symptomless carrier of this virus. Therefore, it was shown that interveinal mosaic virus did not protect

**The potato varieties used were from indexed tuber units obtained from Melvin Rominsky, Starks Farms Inc., Rhinelander, Wis.

FIGURE 1.—Typical systemic symptoms at 18° C. on potato following inoculation with interveinal mosaic virus from seedling 41956 by means of the peach aphid. A, Green Mountain. B, Irish Cobbler.

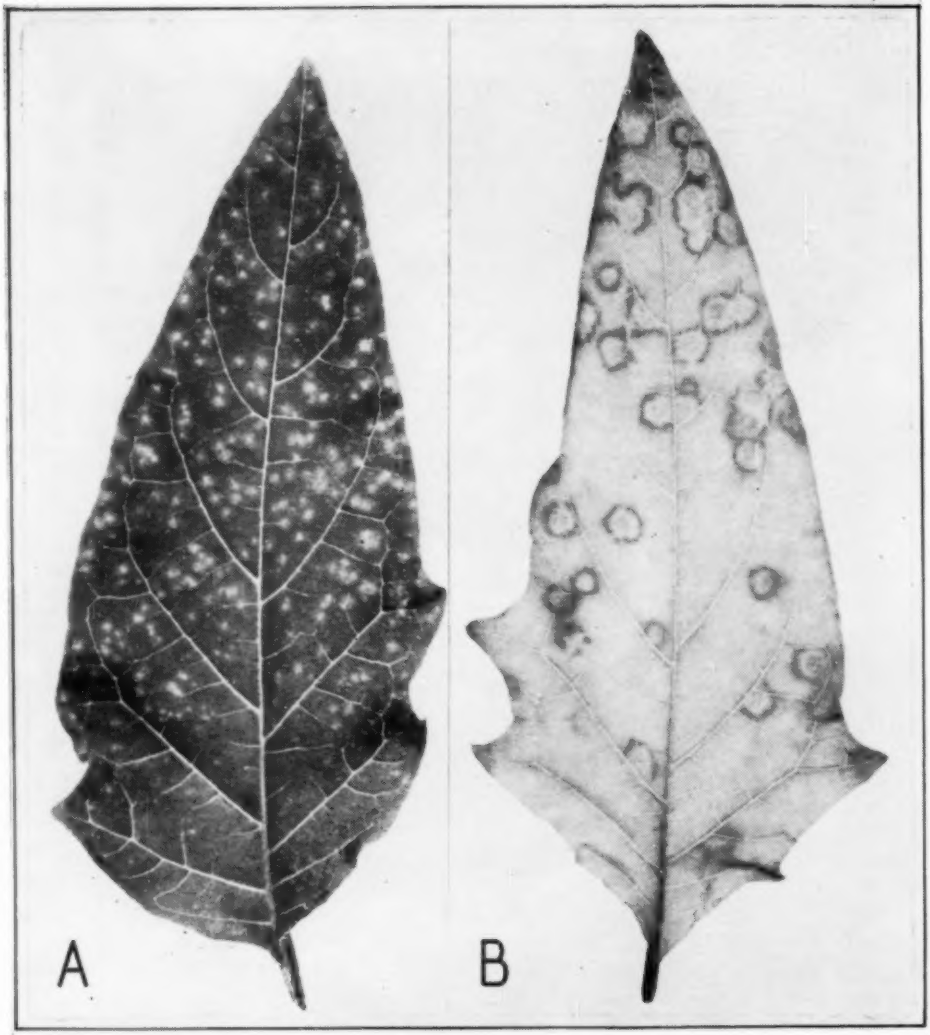

FIGURE 2.—Systemic reaction of *Datura stramonium* var. *tatula* graft-inoculated with interveinal mosaic virus. A, Early symptoms consisting of distinct chlorotic lesions. B, Later stage on chlorotic leaves consisting of distinct dark green circular lesions with chlorotic centers.

against further infection with virus A, and that no synergism occurred between these viruses.

Interveinal mosaic virus, which systemically infects the varieties Irish Cobbler, British Queen and Green Mountain, was investigated. Since Irish Cobbler and British Queen, which are top-necrotic, and therefore field immune from virus A were susceptible to infection with interveinal mosaic virus, it was thought that this virus was either a mutant of virus A or a distinct virus. *D. stramonium* var. *tatula* and *D. ferox* reacted to graft inoculation with interveinal mosaic virus by the formation of chlorotic lesions, and *N. physaloides* proved to be a symptomless carrier. In cross protection tests *N. physaloides* plants infected with interveinal mosaic virus were susceptible to further infection with virus A. The systemic infection of both Irish Cobbler and British Queen on inoculation with interveinal mosaic virus, the reaction of the 2 *Datura* species to graft inoculation, and the failure to cross protect against virus A, indicate that the interveinal mosaic virus is not a strain of virus A. The problem of inter-relation of the interveinal mosaic virus and other potato viruses (virus A and leaf rolling mosaic) is being investigated.

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POTATO NEWS AND REVIEWS

TIME, METHOD OF APPLICATION, AND PLACEMENT OF FERTILIZER FOR EFFICIENT PRODUCTION OF POTATOES IN NEW ENGLAND[1]

Arthur Hawkins[2]

The potato is one of the most responsive crops to fertilization in the Northeast. In most sections where potatoes are produced commercially, a ton or more of "single strength" analysis fertilizer is the rule and normally the return from its use justifies heavy applications.

Factors in Efficient Fertilization of Potatoes

Most growers are interested in deriving maximum efficiency from the fertilizer used for the potato crop. Among the most important factors which he should consider in the use of fertilizer are (1) the optimum amount of nutrients to obtain desired yields and quality, (2) suitability and cost of materials, and (3) time, method of application, and placement.

Recent experiments in Maine have been summarized (12, 13, 23) showing that the response of potatoes to applications of phosphorus and potash was related to the amount of readily soluble phosphorus and potash in the soil. The results of these tests indicate that considerably more phosphorus and potash are applied by most growers than is necessary for maximum yields and quality. More recently, the response of potatoes to nitrogen in Maine and Connecticut have been summarized (15, 22). The optimum amounts of nutrients to supply for a given soil as affected by past use of land and/or soil tests have been suggested in these publications and in others (13, 16) for more efficient fertilization of potatoes.

Time, Method of Application, and Placement of Fertilizer

An attempt will be made to review some of the experimental results on time, method of application, and placement of fertilizer, especially those conducted in New England, for efficient production of potatoes. Time, method of application, and placement of fertilizer for potatoes can be subdivided into two general headings: (A) Complete fertilizer applied just before or at time of planting, and (B) Placement of individual plant nutrient carriers.

A. Complete Fertilizer Applied Just before or at Time of Planting

1. *Row versus Broadcast Applications*

The earliest fertilizer placement work largely involved the general methods of broadcast *versus* row applications without apparent need for precise placement of fertilizer in relation to seed. One of the first reports on fertilizer placement research with potatoes issued by the Hatch Experiment Station in 1894 (18) stated that application in the row

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was found to be superior to broadcasting the fertilizer. Other workers (1, 10, 17) reported superior yields with row application compared to broadcasting, particularly at the lower rates of fertilizer application.

Odland and Damon (20) report that yields obtained from broadcast application were considerably below any of those obtained with four different methods of placement in the furrow in Rhode Island experiments during the period 1926-1931. These comparisons were made using approximately 2000 pounds 5-8-7 per acre.

Cooke (8) reporting on recent work on methods of applying fertilizer to potatoes in England 1945-1947, states that broadcasting fertilizer on the land before it was ridged up for planting resulted in inefficient use of fertilizer. It took 1500 pounds of 7-7-10½ broadcast to equal 1000 pounds applied in or near the row.

Placing the fertilizer in the row, especially in narrow bands, *reduces phosphate fixation.* This is of special importance in potato fertilization in the Northeast *since most potato soils are kept highly acid to control scab.* Iron and aluminum which precipitate phosphorus are more active on highly acid soils. Besides, fertilizer placed near the seed is more accessible to the plant than if placed otherwise.

The response of potatoes to row placement of fertilizer as compared with broadcast application would be expected to be affected by the rate of fertilizer application and the nature of the soil, including nutrient supply before fertilization, leachability, degree of acidity, and phosphorus fixing capacity.

2. *Comparisons of Different Placements in the Row*

With potato fertilizer mixtures gradually changing to include the use of more soluble salts and with increasing rate of application, damage to seed and the plant in its early stage of growth was observed with some row applications.

Coe (7) in 1922 studied several fertilizer placements, and with applications of 1950 pounds per acre of 4-10-4 obtained the highest potato yield when the fertilizer was placed in a continuous band 1 to 2 inches to each side of and a little below the level of the seed. The lowest yield resulted from furrow application of fertilizer in contact with the seed. Truog, *et al* (24) using applications of 1000 pounds per acre of 4-8-6 and 4-7-6 fertilizer, favored a placement one-half inch to each side of the seed and also immediately under the potato seed piece.

Cooperative field investigations on fertilizer placement for potatoes conducted during the period 1931-1937 on important soil types in Maine, Michigan, New Jersey, New York, and Ohio were summarized by Cumings and Hougland (11). The chief comparisons were as follows: (a) fertilizer in bands on each side of and level with the seed piece at distances of 1, 2 and 4 inches, (b) in bands on each side and 2 inches below seed piece level, (c) over seed piece, (d) in band underneath seed piece, with 1 to 2 inches of fertilizer-free soil interposed, (e) in furrow, lightly mixed with soil, and (f) in furrow well mixed with soil. Rates of 2000 pounds per acre of 4-8-7 and 5-8-7 were used in Maine and Long Island, respectively.

In 23 out of 27 experiments, side placement of fertilizer resulted in higher yields than other methods of application. Placement of the

fertilizer in a band immediately under or above or mixed with the soil around the seed piece usually resulted in delayed emergence of the sprout and reduction in yield. Fertilizer placed in a band at each side of the row resulted in the most rapid emergence of sprouts and most vigorous plant growth.

The recommendation covering the placement of fertilizer for potatoes as given in the publication by Cumings and Hougland (11), and included in the recommendations of The National Joint Committee on Fertilizer Application, April, 1938, is as follows:

> POTATOES: Fertilizer should be applied in bands on each side of the seed piece with two inches of fertilizer-free soil interposed. The fertilizer bands should be on a level with or slightly below the seed piece. On sloping land, in order to avoid fertilizer shifting too close to the seed, it is recommended that the depth of fertilizer placement be about an inch below the seed level.

More recently, Cooke (9) in England reporting on results of 29 experiments conducted 1945-1947, recommends side placement for efficient utilization of the fertilizer for applications normally required to give maximum yields. In wet or normal rainfall years, observations on the growing crops revealed no harmful effects of fertilizer placed in contact with the seed. In an abnormally dry year, 1947, however, growth was severely checked at several locations by heavy fertilizer applications placed in contact with the seed and the final yields were below those from fertilizer placed in side bands which caused no early check. Placement in one band 2 inches below the seed was tested in four experiments and proved inferior to other placement methods and to broadcasting over the ridges.

Use of One Side-band. Cumings and Hougland (11) report that placement of all the fertilizer in one band at one side of the row gave lower yields in some cases than a band at each side.

Hill Placement. They (11) also report that the use of broken bands or hill placement of fertilizer in short bands at each seed piece or hill gave no indication of advantage over comparable placements in continuous bands along the row for seed spacing ranging from 12 to 16 inches.

Hi-Lo Placement. Since the general adoption of the recommended method, other methods have been suggested for the potato crop. The so-called Hi-Lo method was reported to have an advantage from placing one of the fertilizer bands 2 to 3 inches below the seed piece level into usually more moist soil for the purpose of maintaining greater nutrient availability under low rainfall conditions. Another suggested change involved placing 75 per cent of the fertilizer in the lower band and 25 per cent in the upper band. Results of experiments in New Jersey and Aroostook County (4) over a three-year period showed no advantage of the Hi-Lo methods. Since a larger disk is required for the low side, mechanical difficulties were experienced in attempts to place fertilizer 2 to 3 inches below the seed piece level on rocky soil.

3. *Broadcasting Part of the Fertilizer versus Placing All in Bands*

Fertilizer placement tests with potatoes comparing plow-under treatments with standard fertilizer placement (row side-bands) were conducted

on Caribou loam soil at Aroostook Farm, Presque Isle, Maine, in 1943 and 1944 (5, 6). This soil, which had been planted frequently to potatoes, contained 200 pounds Truog available P_2O_5 and 475 pounds exchangeable potash per acre, was about average of soils planted to potatoes in central Aroostook County at that time (12).

In these tests the total amount of nutrients applied per acre in each case was 2000 pounds 6-6-12. The Green Mountain variety was grown in 1943; Chippewas and Green Mountain on split plots in 1944.

The placements included broadcasting all the fertilizer before plowing, plowsole placements, broadcasting all the fertilizer after plowing, and combinations of plow-under placements and row applications, in comparison with all of it placed in side-bands.

Although some of the placements or combinations resulted in yields as good or slightly better than all in the side-bands, none was consistently superior in either a wet (1943) or a dry (1944) season. In the 1944 trials when three-fourths of a complete fertilizer was broadcast and plowed under or furrow-bottom placed, significantly lower yields occurred with the relatively shallow-rooted Chippewa variety. The reductions in yield to furrow-bottom placements with the deeper-rooted Green Mountain variety were not significant. Under the conditions of these experiments, there was no advantage in varying the placement from applying all the fertilizer in side-bands.

Brown in Connecticut (2) found that the application of all the phosphorus on the plow sole resulted in greatly retarded early growth and a 10 per cent reduction in yield as compared with side-band placement. None of the plow-sole treatments resulted in better stands, growth or yields than the same amount applied in side bands.

B. Placement of Individual Plant Nutrient Carriers

1. *Effect of Placement of Nitrogen on Potato Yields*

Experiments were started in Connecticut in 1948 (15) to compare the application of part of the nitrogen either broadcast or side-dressed with applying all the nitrogen in the row side band placement. In all cases the same amounts of phosphoric acid and potash (180 pounds each of P_2O_5 and K_2O per acre) were added in side bands at planting time with the row applications of nitrogen.

a. *Part of the nitrogen carrier broadcast as compared with all in side-band placement at planting time.*

Connecticut: Comparisons were made in 1948 in Connecticut (15), using sulfate of ammonia as a source of additional nitrogen applied either broadcast or all in side-bands. Broadcast applications of 60 or 90 pounds of nitrogen were disked in previous to planting. An additional 90 pounds from various sources in the complete fertilizer were band-placed in the row at the time of planting. These were compared with 150 or 180 pounds per acre of nitrogen applied all in the row at time of planting.

There was no advantage in yields obtained from broadcasting part of the nitrogen fertilizer (sulfate of ammonia). In fact, decreased yields were obtained on two of the four farms when part of the nitrogen was broadcast and harrowed in previous to planting.

The reduction in yields from broadcast application of nitrogen might have been due either to the greater leaching or to surface run-off of nitrogen, or to the greater effect on soil acidity of sulfate of ammonia when mixed through the soil. This highly acid-forming source of nitrogen has been found to increase toxic conditions on excessively acid soils, especially those low in organic matter (14).

Maine: In Maine, applications of 150 and 180 pounds of nitrogen per acre applied in row side-bands at planting were compared with 90 and 120 pounds applied in row side-bands plus 60 pounds broadcast in 1949-1950 (22). Lower average yields resulted in some cases from the split applications of nitrogen, especially at the 150-pound rate. The authors suggested that apparently the nitrogen applied broadcast was not utilized as well by the crop, possibly because the roots either did not contact the nitrogen as well or more nitrogen was dissolved and carried away by surface run-off than was the case with the row application.

b. *Part of the nitrogen side-dressed as compared with all nitrogen in side-bands at planting time.*

Connecticut: On fine sandy loam soils in Connecticut, the application of additional nitrogen for potatoes in the form of ammonium nitrate as a side-dressing when the plants were 6 to 10 inches high was compared with additional nitrogen from Uramon applied in a complete fertilizer in the row in 1949 and 1950 (15). Sidedressing with 60 or 90 pounds of nitrogen per acre resulted in the plants remaining equally green late into the season and with about the same increases in yields as where all of the nitrogen was placed in side-bands at planting time.

In the four experiments conducted in 1950, comparisons were also made with castor pomace (5.5 per cent nitrogen) broadcast just previous to planting. As good yields were obtained from an additional 60 pounds of nitrogen whether applied as a side dressing of ammonium nitrate or from castor pomace broadcast or from additional Uramon applied all in the row at planting time.

Maine: Deferred applications of part of the total nitrogen as a side-dressing when the plants were about 12 inches high, as compared with all of it applied at planting time, resulted in decreased yields in two Maine experiments in 1949 (22). On the basis of these results it was suggested that with a short growing season, late side-dressed applications of nitrogen would place the plant at a greater disadvantage than in regions with a longer growing season. The Maine results indicate that the side-dressed applications may have been deferred too late.

The advantages of side-dressed applications of nitrogen include: (1) the opportunity to use more of the less expensive sources of nitrogen, such as ammonium nitrate, (2) reduction in the amount of nitrogen subject to leaching, *particularly on sandy soils*, prior to time of usage by the plant.

C. Part Applied as Foliar Application

Results of work in Maine in 1949 indicate response of potatoes to added nitrogen applied as a foliar application of urea. The amount of information available on foliar application of nitrogen as a means of supplying part of the nitrogen for potatoes is very limited.

2. *Phosphorus Carrier*

a. *Phosphorus carrier around or over seed with nitrogen and potash ingredients in side bands compared with application in complete fertilizer in side bands.*

Brown, *et al* (3) report results of experiments in Virginia in 1936 and 1937 with separate fertilizer ingredients (2000 pounds 6-6-5) applied either in the furrow or side placement on Sassafras sandy loam.

The highest yields were obtained where the nitrogen and potash ingredients were applied in side-bands and the 18 per cent superphosphate was applied in the furrow in partial contact with the seed piece. This divided placement resulted in an average yield increase for the 2-year period of 27.5 bushels above the 166.0 bushel-yield with a complete fertilizer applied in a band on each side of the seed piece.

Maine: The preceding experiment suggested experiments in Aroostook County in attempts to increase the efficiency of phosphatic fertilizers. Placement of pulverized triple superphosphate for potatoes was compared on four farms in Aroostook County, Maine, in 1947 (23).

Regular side-band placement of all or part of the triple superphosphate with nitrogen and potash carriers was compared with spreading all or part of the triple superphosphate in a band 3-4 inches wide in an opened furrow either below or above the potato seed piece with approximately ¼" of soil interposed. On soils low to medium in readily soluble phosphorus, potato yields were slightly lower, significantly so, when 80 pounds P_2O_5 per acre rate was applied near the seed than when it was applied in side-bands. On three of four farms a divided application of 80 pounds P_2O_5 above the shallow-covered seed and 80 pounds in side bands resulted in slight but not significant increases in yields over applying 160 pounds P_2O_5 per acre rate all in side bands. No comparisons were made of applying all the superphosphate at the 160 pound P_2O_5 rate over the seed.

Connecticut: Phosphorus placement tests in Connecticut were an outgrowth of results of experiments by the Storrs Agricultural Experiment Station on a formerly productive soil which had become extremely toxic to potatoes (14). In these experiments Katahdin potatoes showed marked response to heavy applications of lime and/or organic matter. Heavy applications of superphosphate plus moderate lime applications were found to reduce the soluble aluminum content of the soil markedly, and resulted in normal growth and fairly good yields.

Experiments on this soil in 1951 and 1952 showed that increased yields were obtained by applying the superphosphate in an 8-inch band over the shallow-covered seed instead of in side bands with the other fertilizer materials.

At another location in 1952, where the soil had become less productive for potatoes, small increases in yield were obtained with the Green Mountain variety and especially with the Katahdin variety, by applying all the superphosphate over the shallow-covered seed instead of in side-bands with the nitrogen and potash carriers. This soil which had a pH of 5.0 and tested very high in soluble aluminum, had been planted every year to potatoes for approximately 15 years prior to rye in 1951.

In 1953, at three locations where the soils had shown no toxic problem and were medium to medium high in available phosphorus by the Morgan

method, no increases in yield were obtained by applying the superphosphate in an 8 to 10-inch band over the shallow-covered seed with the nitrogen and potash carriers in side bands, as compared with side placement. However, at two of these locations with fine sandy loam soils with pH of 5.8 and 6.0, testing medium high in available phosphorus and only medium in soluble aluminum, yield increases with 100 pounds P_2O_5 per acre over no phosphorus were relatively small.

On newly cleared land, pH 5.0 and testing very low in available phosphorus and very high in soluble aluminum by the Morgan method, increased yields to approximately 15 per cent were obtained when the heavier rates of application of superphosphate were applied over the seed as compared with side-band placement in a complete fertilizer.

The results in Connecticut indicate increased efficiency in use of phosphorus for potatoes when the superphosphate is applied over the shallow-covered seed instead of in side-bands on highly acid soils relatively low in organic matter and testing very high in soluble aluminum.

Summary and Conclusions

The limited experimental results on time, method of application, and placement of fertilizer for potatoes on acid New England soils in a *good state of productivity*, indicate no increases in yields from methods other than applying all the fertilizer in the row in the standard side-placement method described on page 108.

The advantage of row application of the phosphorus carrier over other placements include reduction of phosphorus fixation on *highly acid potato soils* and nearness to the young plant.

However, with heavy rates of fertilizer ,all applied in the row side bands, greater care must be exercised to obtain precise placement to avoid fertilizer injury to the seed and young plant.

A more efficient method of row application of fertilizer for potatoes may be obtained by modifying the all-in-the-row side band placement method as follows:

1. Where inactivation of high amounts of soluble aluminum in soils extremely toxic to potatoes is a problem, superphosphate may be used more efficiently by applying it in an eight-inch band over the shallow-covered seed instead of in side bands.
2. Under Connecticut conditions it has been found that potatoes may be fertilized at less cost by side-dressing part of the nitrogen as ammonium nitrate when the plants are about 6 to 10 inches high. By side-dressing part of the nitrogen, less nitrogen is subject to leaching particularly on sandy soils, as compared with applying all the nitrogen at time of planting.

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ANNOUNCEMENT OF ANNUAL MEETING

The Annual Meeting of the Potato Association of America will be held in conjunction with the American Phytopathological Society at Estes Park Conference Camp, Estes Park, Colorado, August 24-28, 1954.

1. LODGING ACCOMMODATIONS:

(a) Lodges and Sleeping Cabins — Rooms for 2 or 4 persons each. For families without children or with 2 small children and individuals who can room together. Indicate any preference for a room mate. No cooking facilities.

(b) Cabins for Families — For families with 2 or more children including families of 4 or more if one child is 11 or older. Cooking facilities in some cabins, however regular conference rate required from head of family plus a slight charge for other family members.

2. DINING ROOM ACCOMMODATIONS:

Three dining rooms available so that all guests may eat at one time.

3. SERVICE — Maid service, towels and all bedding furnished. A hostess shall be in charge of the lodges. Experienced hikemasters, naturalists, guides, horsemen, *etc.*, will be available.

4. RESERVATIONS —

(a) Families (man, wife and children) deadline June 30, 1954. Families with 2 or more children should indicate desire for cabin with cooking facilities if required.

(b) All others must make reservations by July 31.

Send all reservations to Dr. R. H. Porter, Botany and Plant Pathology Department, Colorado A & M College, Fort Collins, Colorado.

5. RATES —

(a) Conference Rates (includes lodging and meals). For adults (12 years and over) \$25.00 each; for children (7 to 11 yrs.) \$21.00 each; (2 to 6 yrs.) \$18.00 each.

(b) Daily Rates (includes lodging and meals). For adults (12 yrs. and over) \$6.50; children (7 to 11 yrs) \$5.50 each; (2 to 6 yrs.) \$4.75 each. All persons attending the meetings of the Phytopathological Society and the American Potato Association, and staying at the Camp will be expected to pay according to the conference rates as listed. Members of families who wish may also pay regular conference rates. Members of families who wish to prepare their own meals may do so, but will be charged a reasonable fee for lodging. In addition, they will pay for the Chuck Wagon dinner if they wish to attend.

(c) The Chuck Wagon Dinner, Wednesday night included in Conference rate. An extra charge will be made for persons who do their own cooking. Their desire to attend this dinner should be noted in reservation request. This will replace the usual banquet.

6. TRANSPORTATION — Purchase railroad and bus tickets to Estes Park; Air line tickets to Denver. The Rocky Mountain Transportation bus serves Estes Park and the Conference Camp.

7. **ENTERTAINMENT** — On Friday afternoon, August 27, arrangements shall be made for a sight-seeing tour into the mountains. We will go to Bear Lake, and up Trail Ridge road (paved) above timberline, to the top-of-the-world at the Continental Divide. This trip, alone, is well worth coming to Colorado to see. Besides the scheduled sight-seeing tour, the following activities will be available for members of families who do not wish to attend the meetings: (1) Hikes over mountain trails led by experienced hikemasters and naturalists. (2) Saddle livery with mountain-trained horses and ponies for children and inexperienced riders, and cowpokes and cowgals. (3) Fishing for trout in a mountain stream is a sport one should not pass up. A visitor's license for three or ten days can be purchased. There are two trout streams close by the camp. (4) Square dancing for all ages. (5) There are a playground and kindergarten cabin for children from 3 to 6 years of age, under experienced kindergarten instructors. (6) Archery, hobby grounds, tennis, riflery, and picnics for teen-agers. (7) Golf privileges, for a reasonable green fee, can be had at the Estes Park Country Club. Check the bulletin board in the Administration Building for scheduled party trips which you can join.

8. **WEATHER** — Normally the days are pleasantly cool, and a typical afternoon mountain shower may last for a few minutes and be over. Estes Park Conference Camp is at an altitude of approximately 8,000 feet, and the nights are always quite cool. Therefore, *bring along a rain coat and a top coat* regardless of how hot the weather is where you live.

9. **CALL FOR PAPERS** — Titles and abstracts of papers for presentation at the meetings of the Potato Association of America should be sent to Cecil Frutchey, Colorado A & M College, Fort Collins, Colorado, by June 24. A joint session with the American Phytopathological Society is planned. Please indicate length of time required for presentation and your need for projectors, *etc.*

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